Resource distribution mediates synchronization of physiological rhythms in locust groups

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Synchronized behaviour is common in animal groups. In ant colonies, synchronization occurs because active ants stimulate their neighbours to activity. We use oscillator theory to explain how stimulation from active neighbours synchronizes activity in groups of solitary locusts via entrainment of internal physiological rhythms. We also show that the spatial distribution of food resources controls coupling between individual locusts and the emergence of synchronized activity. In locusts (*Schistocerca gregaria*), individual schedules of activity and quiescence arise from an irregular physiological oscillation in feeding excitation (i.e. hunger). We show that contact with an active neighbour increases the probability that a locust becomes active. This entrained activity decreases the time until the locust feeds, shifting the phase of its hunger oscillation. The locusts' internal physiological rhythms are thus brought into alignment and their activity becomes synchronized. When food resources are clumped, contact with active locusts increases, and this increase in the strength of coupling between individuals leads to greater synchronization of behaviour. Activity synchronization might have functional significance in inhibiting swarming when resources are dispersed and accelerating it in more favourable clumped environments.

Keywords: *Schistocerca gregaria*; self-organization; collective behaviour

1. INTRODUCTION

Fireflies flash in unison, cicadas and katydids chirp in time and heart muscle cells contract simultaneously: synchronized behaviour is widespread across taxa and across levels of biological organization. The simplest form of synchronized behaviour arises when individuals all respond in the same way to an external stimulus. In the examples given above, however, synchronization emerges from interactions between individuals in the absence of external driving cues. Stimuli exchanged between neighbours lead to adjustments in their internal self-sustained rhythms that bring these rhythms into alignment. Animal groups can thus synchronize their behaviour if the internal fluctuations that drive the behaviour of individuals are coupled by interactions between them, such that each animal's behaviour becomes entrained to match that of its neighbour (Camazine *et al.* 2001; Strogatz 2003).

Synchronously flashing fireflies are periodic and behave essentially like pulse-coupled oscillators: the visual stimulation from a neighbour's flash resets an individual's internal oscillation. This coupling between individual rhythms brings the entire population into synchrony (Winfree 1987; Goss & Deneubourg 1988; Ramirez Avila *et al.* 2003). Ant activity patterns, by contrast, are irregular (Camazine *et al.* 2001). Mathematical models have shown that even weak coupling can be enough to entrain stochastic oscillators like ants, and to synchronize them. In this case, the frequencies and phases of the oscillations become correlated between individuals, whereas amplitudes remain uncorrelated and unpredictable (Pikovsky *et al.* 2001). This phenomenon has been empirically described in lepto thoracine ants. Individual

ants cycle irregularly between activity and inactivity, and the time interval between activity bouts varies around a characteristic mean duration (Cole 1991a). Interaction with an active neighbour causes a phase shift in an ant's normal activity oscillation and decreases the time until the ant becomes active. This entrainment leads to phase convergence of internal rhythms and hence to synchronization of group activity (Franks *et al.* 1990; Hemerik *et al.* 1990; Cole 1991b; Cole & Cheshire 1996; Cole & Trampus 1999).

In locusts, initiation of activity depends on an irregular oscillation in feeding excitation (*sensu* Simpson 1995). The probability of activity rises with time since the last meal. When an active locust encounters a food source, eating generates negative feedback that reduces excitation, leading to the end of the meal. After the meal, excitation begins to increase again, repeating the cycle. Feeding is not highly periodic because the probability of commencing activity is also affected by a variety of other influences (Simpson & Ludlow 1986). Feeding excitation thus fluctuates over time and contains a significant oscillatory component, generating an irregular cycle of activity and inactivity. The influence of interactions with neighbouring locusts on these cycles has not previously been investigated. However, factors such as light that act as general arousal stimuli have been shown to increase feeding excitation and decrease the latency to feeding (Simpson & Ludlow 1986). Tactile, olfactory and visual cues from neighbours promote activity in locusts (Despland 2001) and crowding appears to increase excitation (Simpson *et al.* 1988). If this is the case, interactions with conspecifics would be expected to decrease a locust's latency to feeding and thus to shift the phase of its

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Table 1. Definitions of variables used in the text.

variable	explanation
t	time since the last meal, in 4 min intervals
d_n	distance to the nearest neighbour, in cm
$\Pr(A)$	probability that A occurs, i.e. that a locust is active
$\Pr(N)$	probability that a locust is in direct contact with an active neighbour
$\Pr(Q)$	probability that a locust is in direct contact with a quiet neighbour
$\Pr(I)$	probability that a locust is isolated, i.e. has no neighbours at $d_n \leq 20$
$\Pr(N_d)$	probability that a locust has an active neighbour at a distance d_n , where $d_n \leq 20$
$\Pr(A \& N)$	probability that both A and N occur; similarly $\Pr(A \& I)$, $\Pr(A \& Q)$, $\Pr(A \& N_d)$
$\Pr(A N)$	probability that A occurs given that N has occurred; similarly $\Pr(A I)$, $\Pr(A Q)$, $\Pr(A N_d)$
h	feeding excitation
$\Pr(f)$	probability of moving to the nearest food patch
d_f	distance to the nearest food patch, in cm
$\Pr(A_e)$	probability of entrained movement = $\Pr(A \& N) + \Pr(A \& N_d)$

internal physiological rhythm. Bringing these rhythms into alignment would lead to synchronization of activity.

Both locusts and ants exhibit irregular cycles of activity, but the underlying physiological mechanisms have only been explored in locusts. This physiologically based model of the control of locust activity cycles provides a biologically meaningful framework for studying how interactions can synchronize the behaviour of a group. Phase-resetting of excitation cycles induced by interactions with conspecifics would provide a physiological explanation for synchronization of group activity.

Desert locusts (*Schistocerca gregaria*) change from a green, quiet, cryptic, solitary form to a black-and-yellow, active, swarming, gregarious form in response to crowding. This change is triggered by mechanical stimulation, that is, by contact between individuals. Solitary locusts tend to avoid one another, and if the food is dispersed, they seldom contact each other. If the food is concentrated in patches, locusts aggregate to feed; contact between individuals increases on crowded food patches and this jostling triggers change to the gregarious form (Collett *et al.* 1998; Despland *et al.* 2000). This effect of resource distribution on contact rate also implies that environmental structure influences coupling between individual locusts' activity rhythms. If entrainment occurs as described above, greater synchronicity of group activity would be expected in clumped than in dispersed environments.

The hypothesis under test is as follows: first, that contact with active neighbours stimulates activity and leads to phase-resetting of the feeding excitation oscillation; second, that resource clumping increases contact rate; third, that resource clumping therefore increases synchronization of locust behaviour.

2. MATERIAL AND METHODS

(a) *Experimental methods*

The experiments were performed on isolated-reared mid-second instar nymphs (1 cm body length)—see Roessingh *et al.* (1993) for details of the rearing method. All the nymphs were food-deprived for 12 h before testing, and marked with a dab of poster paint on the pronotum to distinguish between individuals during the trial.

The experiments were carried out in an enclosed square arena (70 × 70 × 75 cm high). Twenty small pots (1 cm in diameter) of wheat shoots, representing resource patches,

were placed in the arena in one of three patterns: dispersed (pots scattered at random), medium (pots concentrated in a few clumps) or clumped (all pots in a single clump—see Despland *et al.* (2000) for images of the patterns). Ten locusts were placed in the arena and observed for 8 h, manually recording their position and activity every 4 min. At each time-step, each locust was scored as either quiescent, active or eating. Jostling by an active neighbour was recorded when a locust was kicked or antennated, and direct contact with a quiet neighbour was recorded when two locusts were in physical contact but not moving. Four replicates were done for each distribution pattern. See Despland *et al.* (2000) for further details of the experimental procedure.

(b) *Analysis*

To test the first prediction, the probability of being active was compared between locusts in direct contact with active neighbours, locusts in direct contact with quiet neighbours and isolated locusts. The probability of A occurring (e.g. a locust is active), given that N has occurred (e.g. the locust has been jostled by an active neighbour), is given by $\Pr(A|N) = \Pr(A \& N) / \Pr(N)$, where $\Pr(A \& N)$ is the probability that both events occur (Papoulis 1991). If A and N are independent, that is, if the probability of A occurring does not change when N occurs, then $\Pr(A \& N) = \Pr(A) \times \Pr(N)$ and $\Pr(A|N) = \Pr(A)$. See table 1 for definitions of variables.

Jostling by an active neighbour could influence a locust through chemical, visual or mechanical cues. The first two could operate at a distance as well (Despland 2001); therefore, we also calculated the probability of being active according to the distance to the nearest active neighbour, $\Pr(A|N_d)$.

To test the second prediction, we compared the probability of contact with an active neighbour, both direct, $\Pr(N)$, and at a distance, $\Pr(N_d)$, between food distribution patterns.

Findings from the first two predictions were used to define parameter values in an individual-based simulation (see §2c).

To test the third prediction, we first compared the occurrence of entrained activity ($\Pr(A_e)$, calculated from $\Pr(A \& N)$ and $\Pr(A \& N_d)$ based on the findings from the first prediction) between vegetation distribution patterns. Next, the simulation was used to examine phase convergence of the underlying feeding excitation cycles, by examining the correlation between excitation states of locusts present

together in the arena. This correlation is expected to be higher when food is clumped.

Finally, as a measure of synchronization, we examined whether more locusts moved at the same time than would be expected by chance, using both the index of dispersion and the departure from the binomial. The index of dispersion of locust activity was compared between the resource distribution patterns for both experimental and simulation data: $I_d = s_n^2/\bar{x}_n$, where $\bar{x}_n$ is the mean number of locusts active per iteration and s_n^2 is the associated variance. Low values of I_d represent random distribution in time of activity, and high values represent synchronization (Cole 1992).

In addition, the frequency distribution of the number of active locusts per iteration (for both experimental and simulation data) was compared between resource spatial patterns using the binomial distribution. If the movements of individuals are independent of one another, this frequency distribution will fit a binomial curve with a mean value corresponding to the mean number of individuals that have moved per time-step. A departure from the binomial indicates significant synchronization.

(c) Modelling

Based on the results from the experiment above, we built a spatial simulation model to test if the observed effects of interactions on the probability of becoming active can explain experimental results on group synchronization, via phase shifting of feeding excitation cycles. Parameter values and behaviour functions were based on empirical measurements, either from this study or previous ones (Roessingh *et al.* 1993; Simpson 1995; Despland 2001).

The computer simulation used a bounded 70×70 two-dimensional arena with food patches distributed according to the same patterns as in the experiment. Time was divided into 120 iterations (representing 4 min intervals), so that rate values measured in the experiment could be used. Simulations were run with 10 locusts placed at random within the arena. Each treatment (i.e. food distribution pattern) was replicated 1000 times.

Model locusts were characterized by their spatial position within the arena and their feeding excitation, h . h represents the probability of initiating movement, and was modelled by fitting proportional hazard models to the frequency distribution of intervals between activity bouts (Simpson & Ludlow 1986). The probability of activity increases with time since the previous meal (t) as follows: $h = \alpha t^{(\alpha-1)} e^\eta$ where α gives the shape of the curve and e^η represents the overall hazard. In the absence of contact with other locusts, $\eta = 0$. The model was fitted to the experimental data, such that with no interactions, the expected value of h , $\langle h \rangle$, is equal to $\Pr(A|I)$ as measured in the experiment: this curve fitting gives $\alpha = 1.15$. The effect of interactions with neighbours was modelled by modifying the parameter η , based on the findings for $\Pr(A|N)$ and $\Pr(A|N_d)$. This corresponds to multiplying the level of feeding excitation at the moment of contact with a neighbour by the excitatory effect of that neighbour (Simpson & Ludlow 1986).

Once a locust has become active, it moves to the nearest food patch with a probability $\Pr(f) = 0.06 + 0.8/d_f$, where d_f is the distance to the food patch. This function was calculated by fitting a curve to the experimental data. Otherwise, the locust moves a distance $M \leq 10$ cm in a random direction and becomes inactive. When a locust arrives at a patch (i.e. $d_f = 0$), t drops by 10 units per time-step; when $t \leq 10$, the locust

moves slightly off the patch and becomes inactive (Simpson 1995). Figure 1 shows a diagram of the simulation.

3. RESULTS

(a) Prediction 1: interactions, entrainment and phase-resetting

Repeated measures analysis of variance showed that the presence of neighbours (within-subjects factor) significantly affected the probability of being active ($F_{2,120} = 53.5$; $p < 0.001$), whereas the food distribution pattern (between-subjects factor) had no effect ($F_{2,117} = 3.2$; $p = 0.14$). The interaction term was not significant ($F_{2,120} = 1.77$; $p = 0.17$). *A priori* contrasts showed that $\Pr(A|Q)$ was not significantly different from $\Pr(A|I)$ ($F_{1,33} = 0.51$; $p = 0.48$) but that $\Pr(A|N)$ did differ significantly from $\Pr(A|I)$ ($F_{1,33} = 5.02$; $p = 0.01$). Thus, active neighbours stimulate activity, but quiet neighbours have no effect (see table 2).

The probability that a locust with a distant active neighbour is active, $\Pr(A|N_d)$, decreases with increasing distance to that neighbour as shown in figure 2b. One-tailed *t*-tests show that $\Pr(A|N_d)$ is significantly greater than $\Pr(A|I)$ for $d_n \leq 5$, where d_n is the distance to the nearest neighbour, in cm ($p = 0.002, 0.001, 0.001, 0.04, 0.008$, respectively, for $d_n = 1, \dots, 5$; $p > 0.05$ for $5 < d_n \leq 20$). Entrainment thus seems to occur at distances up to 5 cm, after which the probability of an individual being active is indistinguishable from that of an isolated individual. The best fitting curve for $\Pr(A|N_d)$ is a power curve and gives the following relationship: $\Pr(A|N_d) = 0.14d_n^{-0.34}$ ($R^2 = 0.87$).

These findings were integrated into the model: when direct contact occurred with an active neighbour, $\eta = 0.75$. This effectively multiplies h by a factor of 2.17, and leads to $\langle h \rangle = \Pr(A|N)$. Similarly, when indirect contact occurred, $\eta = -0.34 \log(d_n) + 1.96$; this leads to $\langle h \rangle = \Pr(A|N_d)$, for $d_n \leq 20$.

We next tested the effects of contact on time to the next meal (Cole 1992). Indeed, meals, when feeding excitation drops to zero, are the only time when the phase of the internal oscillation can be observed. Contact with an active neighbour decreased the mean time until the next meal, from 4.73 (± 0.017 s.e.) to 3.42 (± 0.017 s.e.) intervals ($t_{988} = 2.83$; $p = 0.005$), although no difference was observed in the mean time spent feeding. Jostling thus generally leads to feeding, which resets the phase of the internal oscillation to the zero point.

(b) Prediction 2: vegetation distribution and contact rate

The probability of having an active neighbour, $\Pr(N)$, increased when food was clumped (ANOVA $F_{2,117} = 10.3$; $p < 0.0001$; see table 3). Figure 2a shows that long-distance interactions also increased with clumping of food.

Most jostling (i.e. 80–90% for all food distributions) occurred on food patches. Locusts moved preferentially to the closest food patch and therefore, when the food was dispersed, individuals tended to spread out between patches and seldom contacted each other (Despland *et al.* 2000). When food was clumped, contact increased between individuals feeding together on the clump—see Collett *et al.* (1998) for a more detailed explanation of how food distribution influences contact rate.

Figure 1. Schematic representation of the simulation. Rectangles represent the locust's activity states, the circles represent the probability of switching between states and the diamonds represent movement.

(c) *Prediction 3: vegetation distribution and synchronization*

The probability of spontaneous activity did not differ significantly between the three distribution patterns (ANOVA on $\Pr(A \& I)$: $F_{2,117} = 2.80$; $p = 0.07$). The overall probability of entrained activity is given by: $\Pr(A_e) = \Pr(A \& N) + \Pr(A \& N_d)$, where $\Pr(A \& N) = \Pr(A|N) \times \Pr(N)$ and $\Pr(A \& N_d) = \sum_{d=1}^{20} \Pr(A|N_d) \times \Pr(N_d)$. Applying the experimental probabilities given in figure 2 and tables 2 and 3 to these equations shows that the probability of entrained movement increases when resources are clumped (ANOVA $F_{2,117} = 10.3$; $p < 0.0001$; see table 3). Since entrained movement leads to phase-resetting of internal excitation cycles, increases in the probability of entrained movement due to food clumping are expected to increase phase convergence between feeding excitation cycles of locusts together in the arena.

The simulation allowed us to test this prediction. Feeding excitation h , was more strongly correlated between locusts when food was clumped than when it was dispersed (proportion of simulation runs for which h

showed significant positive correlations between locusts present together in the arena (i.e. Pearson's $r > 0.5$, $p < 0.0001$): 8.9% when the food was dispersed, 28.9% for the medium pattern and 35.6% for the clumped pattern). Thus, clumping of food sources tends to bring individual excitation cycles into alignment.

The index of dispersion, for both experimental data and simulation output, showed that, in the dispersed resources treatment, locusts moved independently of each other, but that movement was increasingly synchronized in the medium and clumped treatments (see table 3).

χ^2 -tests show that, for the dispersed food treatment, the frequency distribution of locust movement differed from the expected binomial in only one of the four experimental replicates ($p = 0.34, 0.07, 0.34$ and 0.0004 for the four trials). In the medium clumping treatment, the data differed from the binomial distribution in three of the four trials ($p = 0.00001, 0.00001, 0.00001$ and 0.47). In the clumped resources treatment, all four replicates departed from the expected binomial distribution ($p < 0.001$ in all four cases). The simulation gave similar results:

Table 2. The probability of being active, $\Pr(A)$, is given for isolated locusts (i.e. $\Pr(A|I)$), locusts with quiet neighbours (i.e. $\Pr(A|Q)$) and locusts with active neighbours (i.e. $\Pr(A|N)$). (Standard error of the mean is given in parentheses.)

neighbours	none	quiet	active
$\Pr(A)$	0.06 (± 0.007)	0.07 (± 0.001)	0.13 (± 0.002)

Table 3. For the three resource distribution patterns, $\Pr(N)$ is the probability of having an active neighbour, $\Pr(A_e)$ is the probability of entrained activity and I_d is the index of dispersion, for both experimental and simulation data.

distribution	dispersed	medium	clumped
$\Pr(N)$	0.004 (± 0.002)	0.006 (± 0.001)	0.015 (± 0.002)
$\Pr(A_e)$	0.008 (± 0.001)	0.0013 (± 0.002)	0.021 (± 0.003)
I_d expt	0.45 (± 0.08)	0.67 (± 0.08)	1.06 (± 0.1)
I_d model	0.52	0.83	1.2

the proportion of model runs for which the frequency distribution of locust movement departed significantly from the binomial prediction was 11% for the dispersed food pattern, 47% for the intermediate pattern and 92% for the clumped pattern.

4. DISCUSSION

These findings show that active neighbours stimulate individual locusts to become active. This entrainment leads to phase-resetting of individual feeding excitation cycles and to synchronization of activity. Contact with active neighbours increases when resources are clumped. This increase in contact has previously been shown to promote the change to the gregarious form (Collett *et al.* 1998; Despland *et al.* 2000). The present study shows that this environmentally mediated increase in contact also leads to synchronization of group activity in patchy environments.

The strength of coupling between non-identical irregular oscillators is critical to determining whether they will lock phase and synchronize (Strogatz 2003). In ants, age influences individual activity level and hence the degree of coupling between individuals (Cole 1992). Increasing group size also improves synchronization, as predicted by coupled oscillator theory (Cole 1991c). We show that, for locusts, coupling between individuals increases when food resources are clumped. To our knowledge, this study is the first to examine how the structure of the environment can regulate the emergence of synchronized activity between individuals in a population.

The adaptive value of synchronized group activity in colonies of social insects is not clear and several hypotheses have been proposed (Bonabeau *et al.* 1998). It is also possible that synchronization serves no function at all and is merely an interesting, but neutral, epiphenomenon (Cole 1991c). The functional significance of

Figure 2. Effects of distance to active neighbours on an individual's activity: (a) probability of having an active neighbour $\Pr(N_d)$ for all $d_n \leq 20$ (in cm) and (b) probability that motion is entrained by activity of that neighbour ($\Pr(A|N_d)$ compared with $\Pr(A|I)$). Linear curve fitting on panel (a) gives the following relationships between probability of having an active neighbour and distance: $\Pr(N_d) = 0.0072d_n + 0.0097$ for clumped food, $\Pr(N_d) = 0.0063d_n + 0.0036$ for the medium pattern, and $\Pr(N_d) = 0.0029d_n + 0.0078$ for the dispersed pattern. $R^2 = 0.99$ in all three cases.

entrained movement in solitary locusts is essentially that of an escape response: solitary locusts tend to move away from a moving neighbour, often by performing a long low jump (Despland 2001). At low population density, the condition usually encountered by solitary locusts, this behaviour disperses individuals and thus maintains the population in the solitary form. When individuals are concentrated in a small area due to resource clumping, this escape response promotes synchronization of activity within the population.

Locusts spend most of their time inactive on or close to food patches, interrupted by short periods of locomotion before beginning to feed on the same, or a different, food patch (Despland *et al.* 2000). If food patches are clumped, most locomotion occurs on or very close to the clump of patches. An increase in the number of locusts active simultaneously (as occurs when behaviour is synchronized) would tend to increase the probability of jostling between locusts moving on and around the food clump. Synchronization would increase contact rate and hence accelerate gregarization. If this is the case, entrained movement would have opposite effects in low-density dispersed populations and in clumped groups with high local density, respectively inhibiting gregarization under unfavourable conditions and accelerating gregarization under favourable ones.

Entrainment would thus constitute a positive feedback mechanism, driving contact rate toward either the low or

the high extreme and away from intermediate values, and hence driving the population toward either the solitary or the gregarious form. Recent work suggests that intermediate forms are more vulnerable to predation than either the low-density solitary or the high-density gregarious form (Despland & Simpson 2005). In this context, synchronization of activity could play an important role in modulating contact rate and regulating gregarization at intermediate population densities.

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